

# Apparatus of a Triassic conodont species *Cratognathodus multihamatus* (Huckriede)

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**Abstract.** A Triassic conodont *Cratognathodus multihamatus* (Huckriede) from the pelagic limestone of the Taho Formation in Ehime Prefecture, Southwest Japan is newly reconstructed as an octomembrate apparatus with segminate Pa, angulate Pb, breviform digyrate M, alate Sa, breviform digyrate Sb<sub>1</sub>, extensiform digyrate Sb<sub>2</sub>, bifurcate bipennate Sc<sub>1</sub>, and bipennate Sc<sub>2</sub> elements. Among the elements, the Pb, M, and S series were regarded as those of a septimembrate or octomembrate species *Gladigondolella tethydis* (Huckriede) by previous authors. *Cr. multihamatus* may comprise a lineage of the Gondolellidae; it occurs in the Tethyan realm and ranges from late Spathian or early Anisian to late Carnian.

**Key words:** *Cratognathodus multihamatus* (Huckriede), Gondolellidae, octomembrate apparatus, Taho Formation, Triassic

## Introduction

The form species of conodonts, *Cratognathodus kochi* (Huckriede, 1958), *Cratognathodus posterognathodus* Mosher 1968, *Cypridodella venusta* (Huckriede, 1958), *Diplododella lautissima* (Huckriede, 1958), *Enantiognathus stoppeli* (Bender, 1967), *Cypridodella spengleri* (Huckriede, 1958), *Hindeodella petrae-viridis* Huckriede 1958, and *Hindeodella multihamata* Huckriede 1958 were recovered from the Triassic in various areas of Tethyan realm. These eight form species also occur abundantly in the limestone strata of the Taho Formation outcropped at Tahokamigumi, Shirokawa-cho, Higashiura-gun, Ehime Prefecture in Shikoku. As a result of statistic analysis of conodont fauna with these form species from various levels of the upper Spathian or lower Anisian to middle Anisian and upper Carnian strata of the formation, it has been made clear that these form species are the elements of a conodont skeletal apparatus and *Cr. kochi*, *Cr. posterognathodus*, *Cy. venusta*, *D. lautissima*, *E. stoppeli*, *Cy. spengleri*, *H. petrae-viridis*, and *H. multihamata* are assigned to the Pa, Pb, M, Sa, Sb<sub>1</sub>, Sb<sub>2</sub>, Sc<sub>1</sub>, and Sc<sub>2</sub> elements, respectively.

I propose *Cratognathodus multihamatus* (Huckriede) herein for this octomembrate apparatus and describe the elements of the apparatus. Furthermore, I scrutinize the phylogeny of this species and compare it with the previously reconstructed Triassic and some Paleozoic conodont apparatuses.

All of the described specimens are kept in the Department of Science Education, Faculty of Education and Human

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## Biostratigraphic setting

The limestone strata of the Taho Formation attain approximately 75 m in thickness and correspond to Griesbachian to middle Anisian and upper Carnian to lower Norian. Upper Anisian to lower Carnian strata are missing due to a fault (Koike, 1996).

In the Taho Formation, *Cratognathodus multihamatus* ranges from the uppermost part of the *Neospathodus homeri* Zone in the upper Spathian or the basal part of the *Chiosella timorensis* Zone in the lower Anisian to the *Metapolygnathus nodosus* Zone in the upper Carnian. The elements of this species are particularly abundant in the lower Anisian where 930 specimens were recovered from approximately 5 kg of limestone from level 1197. On the other hand, they are very rare in number and poor in preservation in the upper Carnian (Table 1).

*Cratognathodus multihamatus* is a Tethyan species and the elements of the species were reported as form species from various parts of the Tethyan realm by many authors. In the biostratigraphic study of conodonts in Austria, Huckriede (1958) proposed and described the form species *Prioniodina kochi*, *Lonchodina venusta*, *Roundya lautissima*, *Lonchodina spengleri*, *Hindeodella petrae-viridis*, and *Hindeodella multihamata*. These species are assigned to the Pa, M, Sa, Sb<sub>2</sub>, Sc<sub>1</sub>, and Sc<sub>2</sub> elements of the *Cr. multihamatus* apparatus, respectively. The form species *Ozarkodina saginata* de-

**Table 1.** Occurrence of Pa, Pb, M, Sa, Sb<sub>1</sub>, Sb<sub>2</sub>, Sc<sub>1</sub>, and Sc<sub>2</sub> elements of *Cratognathodus multihamatus* (Huckriede) obtained from 3 to 5 kg of limestone of the Tahoe Formation.

Stratigraphic level	Elements								
	Pa	Pb	M	Sa	Sb <sub>1</sub>	Sb <sub>2</sub>	Sc <sub>1</sub>	Sc <sub>2</sub>	Sc <sub>1</sub> ? + Sc <sub>2</sub> ?
Carnian									
1133	13	10	3	2	1	2	5	1	3
Anisian									
1202	31	50	49	9	27	13	11	20	51
1199	14	9	9	2	9	8	2	2	4
1198	29	20	8	5	3	4	4	9	8
1197	242	126	150	18	82	51	19	164	79
1196	20	6	9	3	6	14	3	12	12
1195	38	18	28	6	8	9	6	29	13
1324	23	5	6	3	4	4	1	4	7
1132	18	5	14	2	10	11	10	10	8
1194	52	13	26	5	10	12	8	18	11
1323	63	31	35	3	17	29	7	30	15
016	29	28	21	8	9	31	8	50	19
1193	143	45	38	12	33	36	17	54	39
1130	74	40	17	5	21	27	10	29	30
1322	70	32	25	6	18	25	8	17	36
1129	95	32	45	17	34	49	13	27	38
1321	155	67	68	15	43	65	19	55	29
015	45	14	7	3	12	13	2	29	13
1192	12	9	11	2	6	3	4	9	7
1128	34	16	16	3	7	9	4	10	16
014	37	19	14	2	3	12	3	14	9
1191	59	48	50	16	29	37	11	18	19
1127	265	113	135	39	72	113	48	63	86
1316	66	35	32	7	23	19	9	22	17
Spathian ?									
013	42	26	26	9	7	11	3	19	12
1183	18	3	6	1	2	8	2	6	2
total	1687	821	845	203	615	495	237	721	583
ratio	8.3	4.0	4.2	1	3.0	2.4	1.2+	3.6+	

scribed by Huckriede (1958) was distinguished from the form species *Cratognathodus posterognathus* Mosher (Pb element of *Cr. multihamatus* apparatus) by its shorter posterior process (Mosher, 1968). The form species *Ozarkodina saginata* illustrated by Huckriede (1958) is, however, probably based on incomplete specimens of *Cr. posterognathus* lacking a part of the posterior process. The specimen of the form species *Apatognathus* sp. illustrated by Huckriede (1958) is poorly preserved but the features of the processes and denticulation agree well with those of the Sb<sub>1</sub> element of *Cr. multihamatus*. According to Huckriede (1958), most of the form species occur commonly in the upper Anisian to Carnian.

Bender (1967) reported Spathian and early Anisian conodonts from Chios and other Greek islands in the Mediterranean Sea and described the Pa, Pb, M, Sb<sub>2</sub>, Sc<sub>1</sub>, and Sc<sub>2</sub> elements of *Cr. multihamatus* as the form species proposed by Huckriede (1958). The specimens of the form species *Hindeodella stoppeli* illustrated by Bender (1967) are incomplete but the features of the lateral processes agree with the Sb<sub>1</sub> element of *Cr. multihamatus*. The Pa and Pb elements occur first in the upper part of the middle

*Neospathodus homeri* Zone (late Spathian or early Anisian) and other elements occur first in the lower or middle part of the lower *N. homeri* Zone (late Spathian).

Mosher (1968) studied Triassic conodonts of Austria, North America, and Germany, and described the form species assignable to the Pa, Pb, M, Sa, Sb<sub>2</sub>, Sc<sub>1</sub>, and Sc<sub>2</sub> elements of *Cr. multihamatus* from the Middle and Upper Triassic limestones in Austria. In part the specimens illustrated as the form species *Prioniodina petrae-viridis* by Mosher (1968, Pl. 116, Figs. 30, 31) are referable to the Sb<sub>1</sub> element. Furthermore, Mosher (1968) reported the occurrence of the Pb, Sb<sub>1</sub>, and Sc<sub>2</sub>? elements in the Middle and Upper Triassic of North America, but did not report any occurrences of the elements of *Cr. multihamatus* in the Muschelkalk of Germany. According to Mosher (1968), all of the elements appear first in the late Anisian and the Pb, M, Sa, and Sc<sub>1</sub> elements range to early Ladinian, but the Pa, Sb<sub>1</sub>, Sb<sub>2</sub>, and Sc<sub>2</sub> elements range to Carnian or Norian in Austria.

In their biostratigraphic study of the Lower to Upper Triassic conodonts in some areas of Europe in the Tethyan

realm, Kozur and Mostler (1972) described the form species referable to the Pb, M, Sa, and Sb<sub>2</sub> elements of *Cr. multihamatus*. One of the specimens of the form species *Hindeodella spengleri* (Huckriede) illustrated by Kozur and Mostler (1972, pl. 7, fig. 11) is referable to the Sc<sub>1</sub> element of *Cr. multihamatus*. Most of the specimens of the form species *Enantiognathus petraeviridis* (Huckriede) illustrated by Kozur and Mostler (1972, pl. 10, figs. 1, 2; pl. 14, figs. 4, 5, 8, 12) are the Sb<sub>1</sub> element of *Cr. multihamatus*. The form species *Cratognathodus kochi*, the Pa element of *Cr. multihamatus*, is regarded as the immature form of the "gladigondolelliform" (Pa) element of *Gladigondolella tethydis* (Huckriede) by Kozur and Mostler (1972). According to them, the biostratigraphic ranges of the elements are within the Ladinian to early Carnian.

In the report on Triassic conodonts from Turkey, Gedik (1975) described the form species referable to the Pa, Pb, M, Sb<sub>2</sub>, and Sc<sub>2</sub> elements of *Cr. multihamatus*. The specimens illustrated by Gedik (1975) as the form species *Hibbardella magnidentata* (Tatge) (pl. 4, figs. 8-10), *Enantiognathus zieglerei* (Diebel) (pl. 5, fig. 3), and *Prioniodina (Frabellignathus) latidentata* (Tatge) (pl. 8, figs. 13-15) are probably referable to the Sa, Sb<sub>1</sub>, and Sc<sub>1</sub> elements of *Cr. multihamatus*, respectively. According to Gedik (1975), all of the elements appear first in the Zone A of the early Anisian just above the *Chiosella timorensis* Zone and range to the late Carnian.

Summarizing the above-mentioned reports, *Cr. multihamatus* is a diagnostic species in the Tethyan realm and ranges from late Spathian or early Anisian to late Carnian as recognized in the Taho Formation.

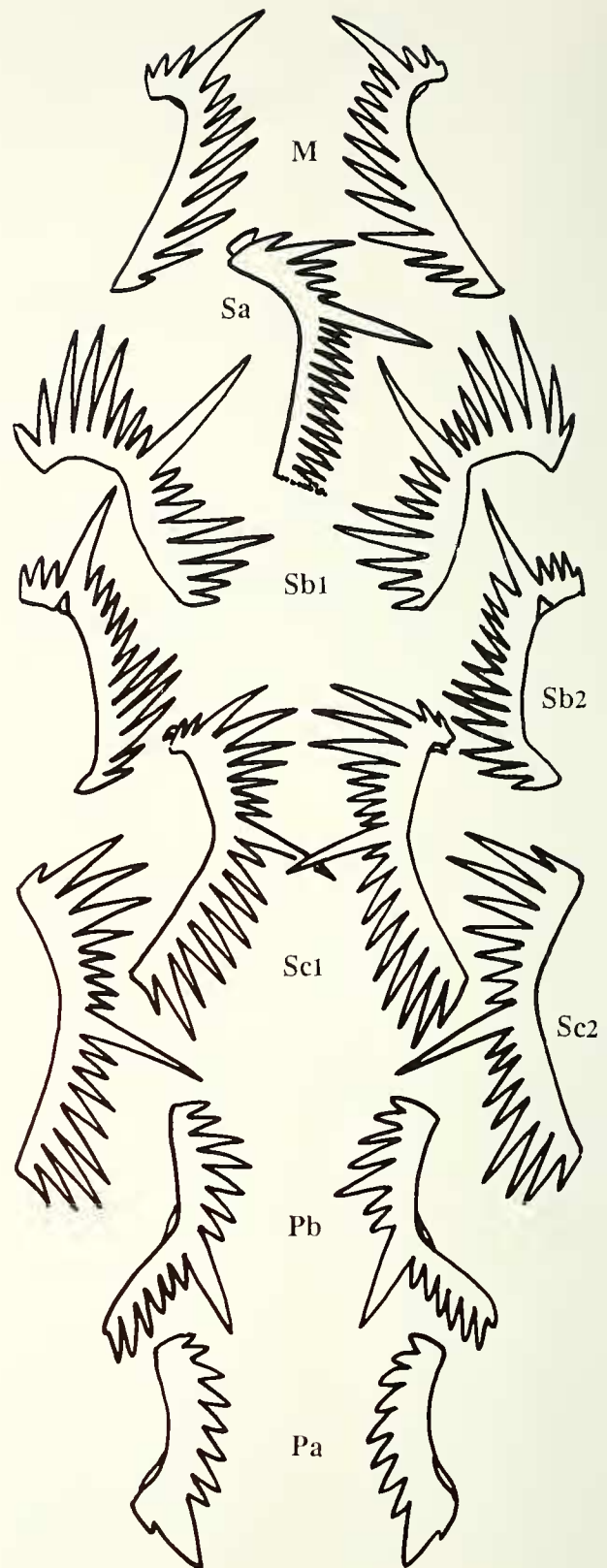
#### Apparatus of *Cratognathodus multihamatus* (Huckriede)

*Cratognathodus multihamatus* is reconstructed as an octomebrate skeletal apparatus in this study (Figure 1). The elements are Pa, Pb, M, Sa, Sb<sub>1</sub>, Sb<sub>2</sub>, Sc<sub>1</sub>, and Sc<sub>2</sub>.

The Pa element is a segminate (neospathodiform) type having an arched anterior process with 3 to 10 relatively short and broad, discrete denticles, a large broad cusp, and an expanded basal cavity. One or two small denticles may be present behind the cusp. It is identical with the form species *Cratognathodus kochi* (Huckriede, 1958).

The Pb element is an angulate (ozarkodiniform) type possessing a strongly and laterally bending unit, an anterior process with 3 to 6 relatively large, discrete denticles, a posterior process with 4 to 6 short, slender, discrete denticles, a large cusp, and a slightly expanded basal cavity. It is identical with the form species *Cratognathodus saginatus* (Huckriede, 1958) and *Cratognathodus posterognathus* Mosher, 1968.

The M element is a breviform digyrate (cypridodelliform) type having a short lateral process with 1 to 3 short denticles, a long lateral process with 8 to 10 short to long denticles, a large cusp, and an expanded basal cavity. It is identical



→ **Figure 1.** A hypothetically reconstructed apparatus of *Cratognathodus multihamatus* (Huckriede) from the Taho Formation.



with the form species *Cypridodella venusta* (Huckriede, 1958).

The Sa element is an alate (diplododelliform) type possessing 2 long lateral processes with 3 to 5 short to long, discrete denticles, a long posterior process with more than 10 short, indiscrete denticles, a large cusp, and a slightly expanded basal cavity. It is identical with the form species *Diplododella lautissima* (Huckriede, 1958).

The Sb<sub>1</sub> element is a breviform digyrate (enantiognathiform) type possessing subequal-sized slender lateral processes with 7 to 10 short to long, discrete denticles, a slender long cusp, and a slitlike basal cavity. It is probably identical with the form species *Enantiognathus stoppeli* (Bender, 1967).

The Sb<sub>2</sub> element is an extensiform digyrate (prioniodiniform) type having a short lateral process with 2 to 5 short denticles, a long lateral process with 10 to 13 short to long, indiscrete denticles, a slender long cusp, and a triangular basal cavity. It is identical with the form species *Cypridodella spengleri* (Huckriede, 1958).

The Sc<sub>1</sub> element is a bipennate (hindeodelliform) type possessing a bifurcate long anterior process with 5 to 8 short to long, discrete denticles, a long posterior process with more than 5 short to long, discrete denticles, a slender long cusp, and a slitlike basal cavity. It is identical with the form species *Hindeodella petrae-viridis* Huckriede, 1958.

The Sc<sub>2</sub> element is a bipennate (hindeodelliform) type having slender long anterior and posterior processes carrying 5 to 12 short to long, discrete denticles, a slender long cusp, and a slitlike basal cavity. It is identical with *Hindeodella multihamata* Huckriede, 1958.

The number of elements of *Cr. multihamatus* occurring in each level is shown in Table 1. The frequencies of the Pa, Pb, M, Sa, Sb<sub>1</sub>, Sb<sub>2</sub>, Sc<sub>1</sub>, and Sc<sub>2</sub> elements from the samples of the Spathian or Anisian to Carnian are 1687, 812, 845, 203, 615, 495, 237+, and 721+, and an approximate ratio of the elements is 8.3:4.0:4.2:1:3.0:2.4:1.2+:3.6+, respectively.

The natural assemblage of *Neogondolella* sp. recovered by Rieber (1980) from the Middle Triassic of Switzerland and *Gondolella pohli* reconstructed by von Bitter and Merrill (1998) based on many natural assemblages from Illinois are composed of a single unpaired alate Sa, single pairs of segminiplanate Pa, angulate Pb, breviform digyrate M, breviform digyrate Sb<sub>1</sub>, and extensiform digyrate Sb<sub>2</sub>, and two pairs of bipennate Sc elements. Orchard (1998) regarded, however, the Sc elements in *Neogondolella* as being composed of Sc<sub>1</sub> and Sc<sub>2</sub>, and the *Neogondolella* apparatus as an octomembrate type.

As mentioned further on, *Cr. multihamatus* represents a close phylogenetic relationship with neogondolellids and is referable to the Gondolellidae. Therefore, *Cr. multihamatus* probably has as many elements as *Neogondolella* sp. (Rieber, 1980) and *G. pohli*. In that case, the abundance of segminate Pa elements is very high compared with other elements in *Cr. multihamatus*. The reason is probably due to robustness of Pa elements. On the other hand, alate Sa elements are considerably low in abundance. This is presumably due to their fragility. The same tendency in abundance of Pa and Sa elements is observed in apparatuses of *G. pohli* (von Bitter and Merrill, 1998, table 1).

### *Cratognathodus multihamatus* and previously reconstructed apparatuses

Kozur and Mostler (1971) reconstructed a multielement species *Gladigondolella tethydis* (Huckriede) with 11 or 12 elements. The elements are identical with the form species *Cr. posterognathus*, *Cy. venusta*, *D. lautissima*, *Cy. spengleri*, *H. petrae-viridis*, *H. multihamata*, *Cr. saginatus*, *Didymodella alternata* (Mosher), *Lonchodina hungarica* Kozur and Mostler, *H. pectiniformis* (Huckriede), and *G. tethydis*. Among these form species, the first six correspond with the Pb, M, Sa, Sb<sub>2</sub>, Sc<sub>1</sub>, and Sc<sub>2</sub> elements of the *Cr. multihamatus* apparatus, respectively. Furthermore, one of the specimens demonstrated as *Enantiognathus petraeviridis* by Kozur and Mostler (1971, pl. 1, fig. 14) is referable to the Sb<sub>2</sub> element of *Cr. multihamatus*.

Hirsch (1981, 1994) also reported a multielement species *G. tethydis* composed of eight elements. Judging from the simple illustration by Hirsch (1994), the eight elements are identical with the form species, *Cr. posterognathus*, *Cy. venusta*, *D. lautissima*, *H. petrae-viridis*, *H. multihamata*, *Cr. saginatus*, *H. pectiniformis*, and *G. tethydis*. As mentioned above, the first five form species correspond with the Pb, M, Sa, Sc<sub>1</sub>, and Sc<sub>2</sub> elements of *Cr. multihamatus*, respectively.

The correlation coefficient of occurrence is very low between the *Cr. multihamatus* apparatus and the Pa element of *G. tethydis* in the Taho Formation: *Cr. multihamatus* appears first at the upper part of the *Neospathodus homeri* Zone in the late Spathian or the basal part of the *Cr. timorensis* Zone in the early Anisian but the Pa element of *G. tethydis* appears later, at the base of the *Paragondolella bulgarica* Zone (Figure 2). Among the studied samples yielding *Cr. multihamatus* (Table 1), the occurrence of the Pa elements of *G. tethydis* is restricted within the levels 1197, 1198, and 1202 in the *P. bulgarica* Zone and the number of the elements found in about 3 to 5 kg of limestone is only 2, 2, and 25, respectively.

According to Muttoni et al. (1998), the Pa elements of *G. tethydis* appear first near the base of the *Paragondolella bifurcata*-*Neospathodus kockeli* Zone in Pelsonian of Anisian of Italy. The first appearance of the Pa elements of *G. tethydis* in Italy is nearly the same in age as their first appearance in Japan. As mentioned previously, *Cr. multihamatus* appears first in the late Spathian or earliest Anisian in Tethyan realm. Therefore, the first appearances of *Cr. multihamatus* and the Pa element of *G. tethydis* are obviously different in the Tethyan realm.

Kozur and Mostler (1972) regarded the form species *Cr. kochi* (=Pa elements of *Cr. multihamatus*) as immature forms of the "gladigondolelliform" (Pa) elements of *G. tethydis*. As mentioned above, mature forms of the Pa elements of *G. tethydis*, however, never occur in the *N. homeri* and *Cr. timorensis* Zones which yield the abundant form species *Cr. kochi*. Furthermore, Pa elements of *Cr. multihamatus* and immature forms of Pa elements of *G. tethydis* are easily distinguished from each other by the feature of lateral expansion of process, denticulation, and the shape of the basal cavity.

As far as observed conodont faunas in Japan are con-

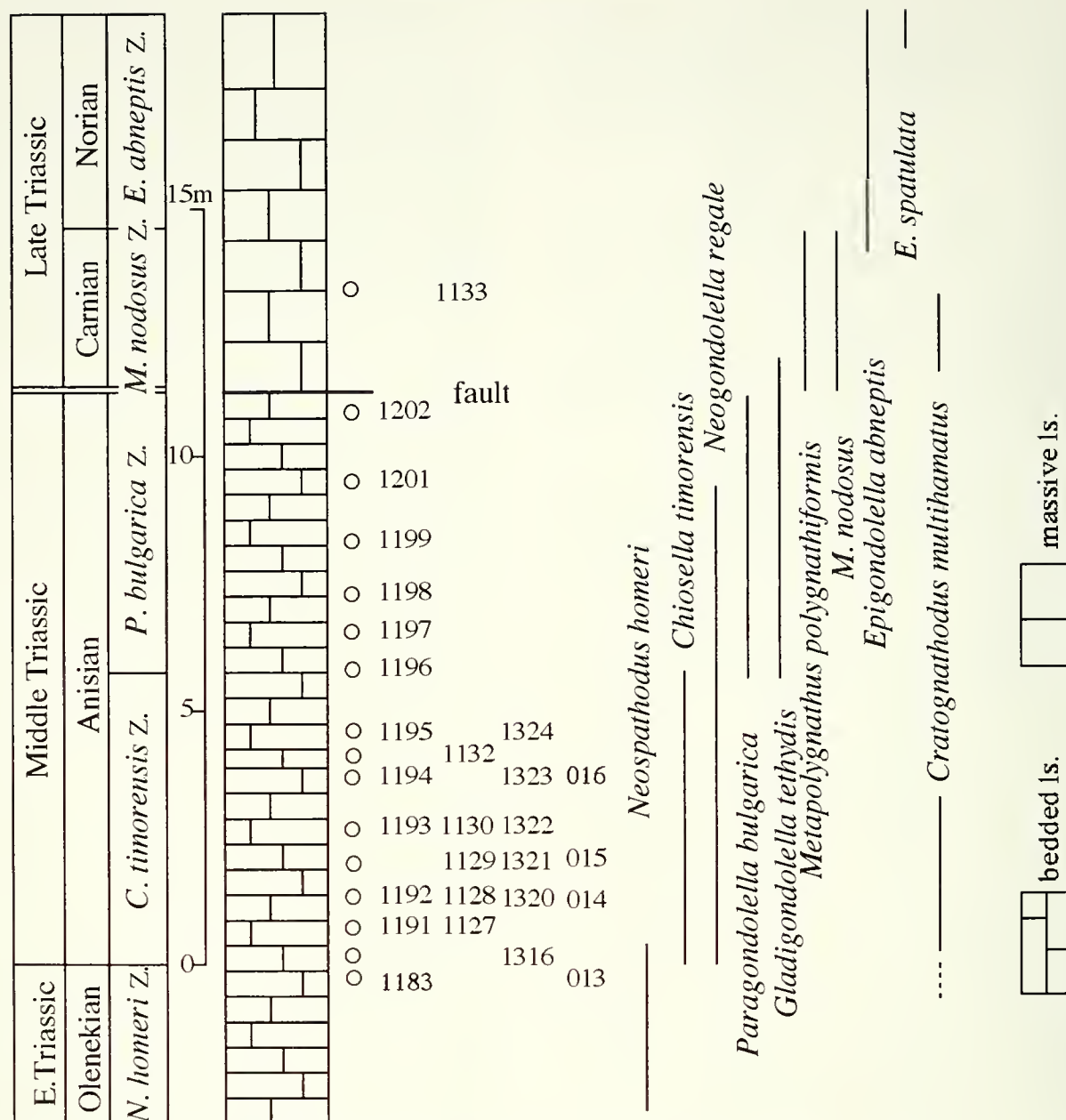


Figure 2. Stratigraphic section and vertical distribution of *Cratognathodus multihamatus* (Huckriede) and important pectiniform conodonts in the Taho Formation.

cerned, the correlation coefficient of occurrence is very low among the Pa element of *G. tethydis* and other pectiniform and ramiform elements. For example, a late Anisian or early Ladinian limestone sample collected from Izuriha near Kyoto yields about 550 specimens of *G. tethydis* Pa elements, but other elements associated with them are mainly of the *Cr. multihamatus* apparatus with some "ozarkodiniform" Pb and a few "enantiognathiform" Sb<sub>1</sub> of unidentified apparatuses. The abundances of the Pa, Pb, M, Sa, Sb<sub>1</sub>, Sb<sub>2</sub>, Sc<sub>1</sub>, and Sc<sub>2</sub> elements of *Cr. multihamatus* in the sample are 19, 56, 36, 17, 30, 59, 72+, and 33+, respectively. Thus, the *G.*

*tethydis* apparatus reconstructed by Kozur and Mostler (1971) and Hirsch (1981, 1994) is problematical. Furthermore, it is difficult to reconstruct *G. tethydis* as a multielement apparatus with Pa and any other elements at present.

#### Phylogeny of *Cratognathodus multihamatus*

As mentioned above, *Cr. multihamatus* is characterized by possessing segminate Pa, angulate Pb, breviform digyrate M, alate Sa, breviform digyrate Sb<sub>1</sub>, extensiform digyrate Sb<sub>2</sub>, bifurcate bipennate Sc<sub>1</sub>, and bipennate Sc<sub>2</sub> elements.



Among these elements, Pa is one of the most important components for scrutinizing the phylogeny of *Cr. multihamatus*.

The Pa element of *Cr. multihamatus* with a relatively large cusp and large discrete denticles is morphologically very different from not only the typical Spathian neospathodid species: *Neospathodus homeri* (Bender) and *N. triangularis* (Bender) but also from the immature forms of the typical Anisian neogondolellid, paragondolellid, and chiosellid species: *Neogondolella regale* Mosher, *Paragondolella bulgarica* (Budurov and Stefanov), and *Chiosella timorensis* (Nogami), all of which exhibit a small cusp and subequal indiscrete denticles. The Pa element of *Cr. multihamatus*, however, represents some morphologic similarities to the immature forms of the Pa elements of *Gladigondolella tethydis*, which appeared later than *Cr. multihamatus* in Anisian time, and *Paragondolella navicula* (Huckriede) and *P. hallstattensis* Mosher, which appeared in Norian time. Furthermore, the Pa element closely resembles the "ozarkodiniform" element of *Celsigondolella watznaueri watznaueri* (Kozur) and the form species *Pollognathus sequens* (Kozur), which are regarded as the endemic Ladinian conodont species of the German Basin (Kozur and Mostler, 1972; Kozur, 1989).

The presence of "enantiognathiform" Sb<sub>1</sub> element in *Cr. multihamatus* is also considerably important in establishing its phylogenetic relationship with the previously reconstructed conodonts. The natural assemblage of *Neogondolella* sp. recovered by Rieber (1980) from the Middle Triassic of Switzerland is composed of as many as 15 elements belonging to Pa, Pb, M, Sa, Sb<sub>1</sub>, Sb<sub>2</sub>, and Sc (von Bitter and Merrill, 1998). The Sb<sub>2</sub> element of *Neogondolella* sp. is of the typical "enantiognathiform" type (von Bitter and Merrill, 1998) and morphologically quite similar to the Sb<sub>1</sub> of *Cr. multihamatus*. The Pennsylvanian *Gondolella pohli* reconstructed by von Bitter and Merrill (1998) based on natural assemblages from Illinois also includes a single pair of "enantiognathiform" Sb<sub>2</sub> elements accompanied by a single unpaired Sa, single pairs of Pa, Pb, M, and Sb<sub>1</sub>, and two pairs of Sc elements.

Orchard (1998) reviewed all gondolellids and pointed out that *Neogondolella* is an octomembrate apparatus with an "enantiognathiform" type occupying the Sb<sub>1</sub> position adjacent to the Sa element and a single pair of Sc elements always having a bifurcate anterior process. Orchard (1998) regarded the Sc element with a bifurcate anterior process as the Sc<sub>2</sub> but now is of the opinion that it is the Sc<sub>1</sub> (personal communication).

In addition to the "enantiognathiform" element, the presence of the Sc element with a bifurcate anterior process in *Cr. multihamatus* represents a phylogenetic relationship with *Neogondolella*. Furthermore, the Pb, M, Sa, and Sb<sub>1</sub> elements of *Cr. multihamatus* also basically have the same morphology as those of *Neogondolella* sp. and *Gondolella pohli*.

The skeletal apparatus of *Pseudofurnishius murcianus* reconstructed by Ramovš (1977, 1978) based on many clusters in the upper Ladinian of Slovenia is setpimembrate with "enantiognathiform" elements. The "pollognathiform" element of *P. murcianus* shows some similarities to the Pa

elements of *Cr. multihamatus*. The "pollognathiform" elements were identified with *Pollognathus sequence* by Ramovš (1977). All elements except for the "pseudofurnishiform" Pa and "chirodelliform" Sb<sub>1</sub>? elements in *P. murcianus* are basically similar to their counterparts in *Cr. multihamatus*.

The Ladinian *Budurovignathus mungoensis* (Diebel) apparatus reconstructed by Mietto (1982) based on clusters from Italy also includes "enantiognathiform" elements with the Pa, M, Sa, and Sc elements.

The *Xaniognathus* and *Cypridodella* apparatuses statistically reconstructed by Sweet (1981, 1988) are composed of six elements such as the Pa, Pb, M, Sa, Sb, and Sc, among which the Pb is regarded as the "enantiognathiform" digyrate type. The Pb element is closely similar to the Sb<sub>2</sub> element of *Neogondolella* sp. of Rieber (1980). Sweet (1988) regarded *Neogondolella*, *Gondolella*, *Xaniognathus*, and *Cypridodella* as belonging to the family Gondolellidae based on the common occurrence of "enantiognathiform" elements among their apparatuses, and as having a close phylogenetic relationship with *Ellisonia* of the family Ellisoniidae, which also bears "enantiognathiform" elements. *Pseudofurnishius* and *Budurovignathus* are as well included in the Gondolellidae by many authors (Sweet, 1988; Kozur, 1989, and others).

Although Dzik (1991) recognized that *Gondolella* is characterized by the presence of lo (enantiognathiform) elements, he claimed the presence of enantiognathiform-like elements in some undescribed apparatuses of the Devonian Hibbardellidae which are unlikely to have any relationships to *Gondolella*.

Sweet (1988) assumed the origin of both of the Gondolellidae and Ellisonidae to be *Idioproniodus* or a closely related genus with "enantiognathiform" elements in the Mississippian. Von Bitter and Merrill (1998) also considered that the Mississippian *Idioproniodus* is a likely ancestor of the Pennsylvanian *Gondolella* based on their recognition of an evolutionary trend of reduction of the posterior process in the anguliplanate Pa elements.

Dzik (1991) pointed out that reduced posterior processes in the platform (p) elements are characteristic of *Gondolella* and a similar feature occurs in some Devonian *Ozarkodina*. On the basis of morphologic similarities in both platform and ramiform elements, Dzik (1991) regarded the Devonian *Pinacognathus* (?) sp. as the probable ancestor of the Gondolellidae.

In summary, I conclude that *Cr. multihamatus* should be included in the Gondolellidae because *Cr. multihamatus* has segminate Pa elements similar to immature forms of some neogondolellid Pa elements and bears "enantiognathiform" Sb<sub>1</sub> elements which are common in the Gondolellidae, and Sc<sub>1</sub> and other elements which are basically similar in morphology to those of neogondolellid and gondolellid apparatuses.

The segminate Pa elements in *Cr. multihamatus* represent close morphologic similarity with the anterior process of the angulate (ozarkodiniform) Pb elements, which are basically the same in morphology as those of *Neogondolella* sp. of Rieber (1980) and *Gondolella pohli*. This feature suggests

that both elements in the P position have a mutual relationship in feeding mechanism, but while the Pa elements acquired broad variation in morphology (anguliplanate *Gladigondolella*, segminate *Neospathodus*, and segmini-planate *Gondolella* and *Neogondolella*), the Pb element remained angulate during the evolution of the Gondolellidae. The ancestral form of the Pa elements of the Gondolellidae may be referable to an angulate (ozarkodiniform) element like the Pb elements.

In that case the ancestor of the Gondolellidae should be searched for in conodonts with "ozarkodiniform"-like Pa and "ozarkodiniform" Pb elements. The conodonts possessing such Pa and Pb elements were not included in the Ordovician family-group of the order Prioniodinida Sweet, 1988 in which the family Gondolellidae was included by Sweet (1988). On the other hand, Ordovician conodonts *Bryantodina? staufferi* Bergström and Sweet and *Plectodina* of Sweet (1988) in the Spathognathodontidae of the order Ozarkodinida Dzik, 1976 possess "ozarkodiniform"-like Pa and "ozarkodiniform" Pb elements (Sweet, 1988).

Dzik (1991) included the order Prioniodinida erected by Sweet (1988) within the order Ozarkodinida and regarded the Gondolellidae as having a phylogenetic relationship with the Spathognathodontidae.

On the basis of morphologic similarity between the Pa and Pb elements in *Cr. multiamatus* and those of the species in the Spathognathodontidae, I would like to support the opinion of Dzik (1991) that the Gondolellidae is phylogenetically related to the Spathognathodontidae of the order Ozarkodinida.

### Systematic Paleontology

Phylum Conodonta  
Order Ozarkodinida  
Superfamily Gondolellacea  
Family Gondolellidae  
Genus ***Cratognathodus***

*Type species.*—*Hindeodella multiamata* Huckriede, 1958, p. 148–149.

*Revised diagnosis.*—*Cratognathodus* newly proposed herein contains species with octomembrate apparatus of as many as 15 elements: single pairs of segminate Pa, angulate Pb, breviform digyrate Sb<sub>1</sub>, extensiform digyrate Sb<sub>2</sub>, bipennate Sc<sub>1</sub> and Sc<sub>2</sub> elements, and a single unpaired alate Sa element. Pa elements characterized by relatively broad cusp with expanded basal cavity and large discrete denticles.

*Remarks.*—Mosher (1968) enacted the genus *Cratognathodus* and included the following four form species in the genus, *Prioniodina kochi* Huckriede, *Cr. posterognathus* newly proposed, and two unidentified species, which are both characterized by the presence of a strong broad cusp with a widely expanded basal cavity, and relatively small number of discrete denticles. As mentioned previously, *Cratognathodus kochi* and *Cr. posterognathus* are respectively identical with the Pa and Pb elements of the *Cr. multiamatus* apparatus. Among the three specimens illustrated as *Cr. kochi* by Mosher (1968), one specimen (pl. 113, fig. 7) is misidentified and another specimen (pl. 113, fig. 4) is not a typical Pa element of the *Cr. multiamatus* apparatus. Mosher (1968), however, regarded the form species *Prioniodina kochi* Huckriede as the type species of his *Cratognathodus*.

Later, Kozur and Mostler (1972) claimed that the genus *Cratognathodus* created by Mosher (1968) is not a valid taxon because the holotype and all other specimens previously described as the form species *Cr. kochi* are immature forms of the "gladigondolelliform" (Pa) elements of *Gladigondolella tethydis* (Huckriede).

Based on my observation on Pa elements of *G. tethydis* from the Taho Formation and other limestone formations in Japan, the immature forms of the element are characterized by a narrow platform-like anterior process and gradually increasing denticles in length toward the anterior as observed in the mature forms. The immature forms of the Pa elements of *G. tethydis* can be, therefore, easily distinguished from the form species *Cr. kochi* (= Pa element of *Cr. multiamatus*).

The Pa element of *Cr. multiamatus* represents various features in the shape and size of the cusp and denticulation on the anterior process (Figure 3). The holotype of the form species *Cr. kochi* (Huckriede, 1958, pl. 12, fig. 11) possessing a short broad cusp and subequal denticles is safely assigned within the range of morphologic variation of the Pa element of *Cr. multiamatus* and agrees well with the specimens illustrated in Figure 3–16, 26.

### *Cratognathodus multiamatus* (Huckriede)

Figures 3–5

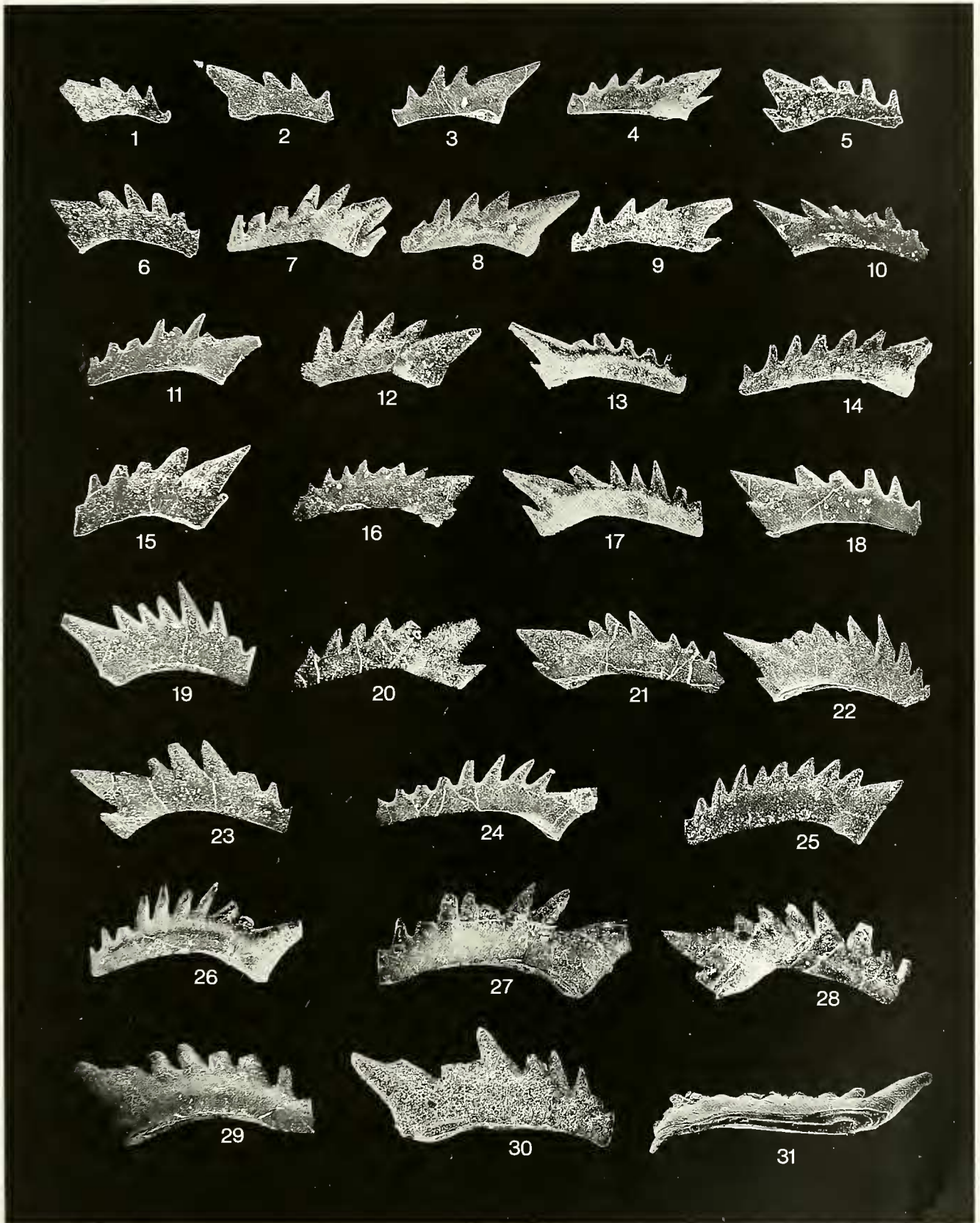
#### Pa element

*Prioniodina kochi* Huckriede, 1958, p. 159, pl. 11, fig. ?37, pl. 12, figs. 11, 12, pl. 14, fig. 4; Spasov and Ganey, 1960, p. 89, pl. 1, fig. 23, pl. 2, fig. 12; Catalov and Stefanov, 1966, pl. 1, fig. 3; Bender, 1967, p. 527, non pl. 5, fig. 12; Hirsch, 1969, pl. 1, fig. ?7.

*Neoprioniodus cf. kochi* (Huckriede), Ishii and Nogami, 1966, non

→ **Figure 3.** 1–31, Pa elements of *Cratognathodus multiamatus* (Huckriede) from the Taho Formation, all  $\times 60$ . 1: YNUC15881 from Lev. 1316. 2: YNUC15882 from Lev. 1195. 3: YNUC15883 from Lev. 1197. 4: YNUC15884 from Lev. 1324. 5: YNUC15885 from Lev. 1196. 6: YNUC15886 from Lev. 1321. 7: YNUC15887 from Lev. 1316. 8: YNUC15888 from Lev. 1127. 9: YNUC15889 from Lev. 1197. 10: YNUC15890 from Lev. 1197. 11: YNUC15891 from Lev. 1191. 12: YNUC15892 from Lev. 1130. 13: YNUC15893 from Lev. 1323. 14: YNUC15894 from Lev. 1183. 15–16: YNUC15895–15896 from Lev. 1321. 17: YNUC15897 from Lev. 1323. 18: YNUC15898 from Lev. 1127. 19: YNUC15899 from Lev. 1321. 20: YNUC15900 from Lev. 1195. 21–24: YNUC15901–15904 from Lev. 1193. 25: YNUC15905 from Lev. 1128. 26: YNUC15906 from Lev. 1321. 27: YNUC15907 from Lev. 1193. 28: YNUC15908 from Lev. 1195. 29: YNUC15909 from Lev. 1193. 30: YNUC15910 from Lev. 1127. 31: YNUC 15911 from Lev. 1320.

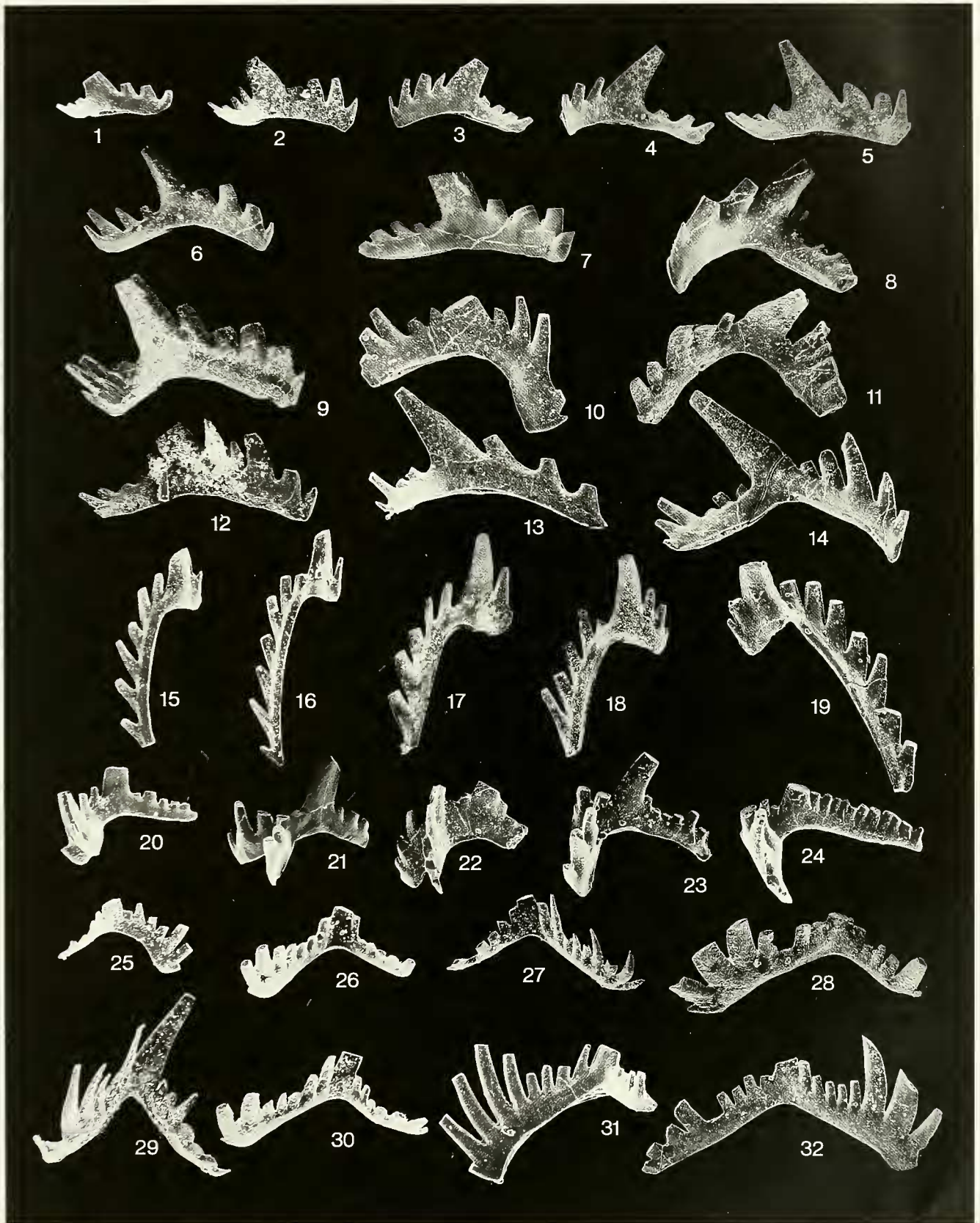






- pl. 1, fig. 12.
- Cratognathodus kochi* (Huckriede), Mosher, 1968, p. 919, pl. 113, figs. 3, ?4, non fig. 7; Jenkins and Jenkins, 1971, non fig. 5, no. 29; Sahni and Chhabra, 1974, p. 263, 265, pl. 3, figs. D, ? E, F, non fig. I; Gedik, 1975, p. 111–112, pl. 5, fig. 23; Budurov, 1976, pl. 4, fig. 29; Sudar, 1977, pl. 5, fig. 4; Catalov and Budurov, 1978, pl. 1, fig. 8; Koike, 1981, pl. 1, fig. 21; Koike, 1982, p. 20, pl. 9, fig. 15, non fig. 16; Önder, 1984, p. 76, pl. 22, figs. ?7, ?8.
- non *Prioniodina? kochi germanica* Kozur, 1968a, p. 139–140, pl. 1, figs. 24, 25; Kozur, 1968b, pl. 3, figs. 15, 19, 21; Kozur, 1968c, p. 1081.
- Cratognathodus cuspidatus* Koike, 1982, p. 20–21, pl. 9, figs. ?17, 18.
- Pb element**
- Ozarkodina saginata* Huckriede, 1958, p. 153–154, pl. 13, figs. 16, 17, 20; Mosher, 1968, p. 932, pl. 115, fig. ?14, non fig. 15.
- Pseudoozarkodina saginata* (Huckriede), Vrielynck, 1987, p. 229–230, pl. 14, figs. 9–11.
- Cratognathodus posterognathus* Mosher, 1968, p. 919, pl. 113, figs. 10, 14; Koike, 1973, p. 98, pl. 17, figs. 30, 31; Budurov and Stefanov, 1975, pl. 1, fig. ?35; Koike, 1981, pl. 1, fig. 30; Koike, 1982, p. 20, pl. 9, figs. 20, 21; Önder, 1984, p. 77, pl. 22, figs. 9–11.
- Lonchodina? posterognathus* (Mosher), Kozur and Mostler, 1971, pl. 1, fig. 10; Mock, 1971, pl. 1, fig. 9; Kozur and Mostler, 1972, p. 19, pl. 10, figs. 6, 7, 11.
- Lonchodina angulata* Budurov, 1971, p. 28, pl. 1, figs. 5–9, 12; Catalov and Budurov, 1975, p. 1248, pl. 1, fig. 8.
- Cratognathodus posterognathus posterognathus* Mosher, Gedik, 1975, p. 112, pl. 5, figs. 19, 20, 22.
- Cratognathodus posterognathus angulatus* (Budurov), Gedik, 1975, p. 113, pl. 8, figs. 25, 26.
- Cratognathodus angulatus* (Budurov), Budurov, 1976, pl. 4, figs. 17, 18; Catalov and Budurov, 1978, pl. 1, fig. 2.
- M element**
- Lonchodina venusta* Huckriede, 1958, p. 152–153, pl. 11, fig. 25; Spasov and Ganev, 1960, p. 82, pl. 1, figs. 15–17; Hirsch, 1969, pl. 1, fig. 5.
- Cypridodella venusta* (Huckriede), Mosher, 1968, p. 922–923, pl. 114, figs. 1, 7, ?13; Gedik, 1975, p. 115–116, pl. 7, figs. 16–18; Koike, 1982, p. 23, pl. 7, fig. 47; Önder, 1984, p. 78–79, pl. 22, figs. 5, 6.
- Prioniodina (Cypridodella) venusta* (Huckriede), Kozur and Mostler, 1971, pl. 1, figs. 3, 4; Mock, 1971, pl. 2, figs. 5, 10, 11; Kozur and Mostler, 1972, p. 32, pl. 11, figs. 16, 24, pl. 12, fig. 11, pl. 15, fig. 3.
- Prioniodina venusta* (Huckriede), Catalov and Budurov, 1975, p. 1248, pl. 1, fig. 12; Budurov, 1976, pl. 4, figs. 23–26; Sudar, 1977, pl. 5, fig. 9; Catalov and Budurov, 1978, pl. 1, fig. 1; Vrielynck, 1987, p. 226–228, pl. 10, fig. 15, pl. 11, figs. 1, 2.
- ? *Cypridodella pronoides* (Budurov), Koike, 1982, p. 22, pl. 7, figs. 48, 49.
- Sa element**
- Roundya lautissima* Huckriede, 1958, p. 160, pl. 11, fig. 41, pl. 13, figs. 13, 15; Spasov and Ganev, 1960, p. 90, pl. 2, figs. 15, 22.
- Diplododella lautissima* (Huckriede), Ishii and Nogami, 1966, pl. 1, fig. 15; Mosher, 1968, p. 924, pl. 114, fig. 20; Koike, 1973, p. 101, pl. 17, fig. 32; Sahni and Chhabra, 1974, p. 270, pl. 3, fig. ?S; Budurov, 1976, pl. 4, fig. 36; Sudar, 1977, pl. 5, fig. 2.
- Hibbardella lautissima* (Huckriede), Mosher and Clark, 1965, p. 561, pl. 65, figs. ?1, ?3, ?4; Kozur and Mostler, 1971, pl. 1, fig. 13; Mock, 1971, pl. 3, figs. 7, 13; Kozur and Mostler, 1972, p. 12, pl. 9, fig. 10, pl. 12, figs. 10, 13; Vrielynck, 1987, p. 195–196, pl. 11, figs. 3–7.
- pars *Hibbardella magnidentata* (Tatge), Gedik, 1975, p. 122–123, pl. 4, figs. 8–10 (only).
- Sb<sub>1</sub> element**
- Apatognathus* sp. Huckriede, 1958, p. 147, pl. 11, fig. 29.
- ? *Hindeodella stoppeli* Bender, 1967, p. 510, pl. 2, figs. 6, 15–17.
- pars *Prioniodina petrae-viridis* (Huckriede), Mosher, 1968, p. 934–935, pl. 116, figs. 30, 31 (only).
- pars *Enantiognathus petraeviridis* (Huckriede), Kozur and Mostler, 1972, p. 9, pl. 10, figs. 1, 2, pl. 14, figs. 4, 5, 8, 12 (only).
- Sb<sub>2</sub> element**
- Lonchodina spengleri* Huckriede, 1958, p. 152, pl. 10, figs. 54, ? 55, ?56, pl. 11, fig. 6, pl. 12, fig. 9, pl. 13, figs. 1, 6, 10, pl. 14, fig. 11; Budurov, 1962, p. 119, pl. 1, figs. ?5–8; Mosher and Clark, 1965, p. 562, pl. 66, fig. ?5; Bender, 1967, p. 513–514, pl. 3, figs. 12, ?13–15, non fig. 17.
- Prioniodina spengleri* (Huckriede), Catalov and Budurov, 1975, p. 1248, pl. 1, fig. ?13, non fig. 14; Sudar, 1977, pl. 5, fig. ?11; Catalov and Budurov, 1978, pl. 1, fig. 5, non figs. 4, 6, pl. 2, fig. 20, non figs. 19, 21.
- Prioniodina spengleri* (Huckriede), “dimitrovi” element, Budurov, 1976, pl. 3, figs. 8, 18.
- Prioniodina spengleri* (Huckriede), “spengleri” element, Budurov, 1976, pl. 3, figs. ?9, ?11–15, 16–18, non figs. 20–25, non pl. 4, figs. 37–39.
- Prioniodina (Flabellignathus) spengleri sapanlii* Gedik, 1975, p. 146–147, pl. 7, figs. 22, 26, 27, 30.
- Cypridodella spengleri* (Huckriede), Mosher, 1968, p. 922, pl. 113, figs. 19, 20, 25, non fig. 18; Koike, 1973, p. 100, pl. 16, fig. 31; Sahni and Chhabra, 1974, p. 269, fig. 3–?O; Önder, 1984, p. 78, non pl. 22, figs. 3, 4.
- Hindeodella (Metaproniodus) spengleri* (Huckriede), Kozur and Mostler, 1971, pl. 1, fig. 12; Mock, 1971, pl. 2, fig. ?13, non fig. 14; Kozur and Mostler, 1972, p. 16–17, non pl. 7, fig. 11, pl. 10, fig. 4, pl. 15, figs. 1, 5.

→ **Figure 4.** Pb, M, Sa, and Sb<sub>1</sub> elements of *Cratognathodus multiamatus* (Huckriede) from the Tahoe Formation, all ×60. **1–14**, Pb elements, 1: YNUC15912 from Lev. 1191. 2: YNUC15913 from Lev. 1321. 3–5: YNUC15914–15916 from Lev. 1130. 6: YNUC15917 from Lev. 1321. 7: YNUC15918 from Lev. 1316. 8: YNUC15919 from Lev. 1321. 9: YNUC15920 from Lev. 1322. 10: YNUC15921 from Lev. 1193. 11: YNUC 15923 from Lev. 1316. 12: YNUC 15924 from Lev. 1197. 13: YNUC15925 from Lev. 1192. 14: YNUC15926 from Lev. 1321. **15–19**, M elements, 15: YNUC15926 from Lev. 1321. 16: YNUC15927 from Lev. 1197. 17: YNUC15928 from Lev. 1323. 18: YNUC15929 from Lev. 1193. 19: YNUC15930 from Lev. 014. **20–24**, Sa elements, 20: YNUC15931 from Lev. 016. 21: YNUC15932 from Lev. 1127. 22: YNUC15933 from Lev. 1129. 23: YNUC15934 from Lev. 1193. 24: YNUC15935 from Lev. 1195. **25–32**, Sb<sub>1</sub> elements, 25: YNUC15936 from Lev. 1197. 26–27: YNUC15937–15938 from Lev. 1196. 28–29: YNUC15939–15940 from Lev. 1197. 30: YNUC15941 from Lev. 1196. 31–32: YNUC15942–15943 from Lev. 1197.





Sc<sub>1</sub> element

*Hindeodella petrae-viridis* (Huckriede, 1958, p. 149-150, pl. 11, fig. ? 46, pl. 13, figs. ?7, ?8, 9, 11, 12, 14, pl. 14, fig. 6, non fig. 7; Spasov and Ganev, 1960, p. 81, pl. 1, figs. 3, 4; Budurov, 1962, p. 116, pl. 1, figs. ?19, ?20; Mosher and Clark, 1965, p. 562, pl. 65, fig. ?9; Ishii and Nogami, 1966, pl. 1, fig. ?14; Catalov and Stefanov, 1966, pl. 1, figs. 4, 7, ?16; Hirsch, 1969, pl. 1, fig. 4.

*Prioniodina petrae-viridis* (Huckriede), Mosher, 1968, p. 934-935, pl. 116, figs. 28, 29, non figs. 30, 31; Sahni and Chhabra, 1974, p. 284-285, fig. 5, ?A, C, ?D, ?E; Sudar, 1977, pl. 5, figs. ?7, ?12; Önder, 1984, p. 86-87, pl. 23, figs. 16-21.

*Prioniodina (Flabellignathus) petraeviridis* (Huckriede), Gedik, 1975, p. 145-146, pl. 8, figs. 11, 27.

*Prioniodina spengleri* (Huckriede), "petraeviridis" element, Budurov, 1976, pl. 4, figs. 38, 39, non fig. 37.

*Parachirognathus petrae-viridis* (Huckriede), Bender, 1967, p. 524, pl. 5, figs. ?1, 2, 3, ?4, ?5, 6, non figs. 8, 9.

*Enantiognathus petraeviridis* (Huckriede), Mock, 1971, pl. 1, fig. 3, non figs. 4, 10, pl. 2, fig. 17; Kozur and Mostler, 1972, p. 9, pl. 10, fig. ?3, non figs. 1, 2, pl. 12, fig. ?16, non pl. 14, figs. 4, 5, 8, 12; Kemper et al., 1976, pl. 6, fig. ?8; Vrielynck, 1987, p. 188, pl. 9, fig. ?10, non figs. 11, 12.

*Diplododella petraeviridis* (Huckriede), Koike, 1981, pl. 1, fig. 26; Koike, 1982, p. 26-27, pl. 7, fig. 25.

*Prioniodina (Flabellignathus) latidentata* (Tatge), Gedik, 1975, p. 143-144, pl. 8, figs. 13-15, ?16-18, ?20, ?21, ?23, ?24.

*pars Hindeodella (Metaproniodus) spengleri* (Huckriede), Kozur and Mostler, 1972, p. 16-17, pl. 1, fig. 11 (only).

Sc<sub>2</sub> element

*Hindeodella multihamata* (Huckriede, 1958, p. 148-149, pl. 10, figs. 52, 53, pl. 12, fig. 23; Catalov and Stefanov, 1966, pl. ?1, fig. 15; Bender, 1967, p. 508-509, pl. 2, figs. ?18, 20; Mosher, 1968, p. 925, pl. 114, fig. 19; Kozur and Mostler, 1971, pl. 1, fig. 9; Koike, 1973, p. 104, pl. 17, figs. 26-29, non fig. 25; Sahni and Chhabra, 1974, p. 274-275, fig. 4, A, D; Budurov, 1976, pl. 4, fig. 40; Chhabra, 1981, pl. 1, figs. 14, 17; Koike, 1982, p. 30, pl. 9, figs. 23, 25, non fig. 24; Vrielynck, 1987, p. 201-202, pl. 14, fig. ?6, non figs. 4, 5.

*Neohindeodella multihamata* (Huckriede), Koike, 1981, pl. 1, fig. 17. *Hindeodella (Metaproniodus) pectiniformis* (Huckriede), Kozur and Mostler, 1972, p. 15-16, pl. 5, figs. 1, 2, pl. 14, figs. 19, ?23, 24.

*Prioniodina (Flabellignathus) pectiniformis* (Huckriede), Gedik, 1975, p. 144-145, pl. 8, fig. 22.

*Prioniodina libita* Mosher, 1968, p. 934, pl. 115, figs. 17, 26, 29; Önder, 1984, p. 86, pl. 23, figs. 13, 14.

**Description.**—Pa and Pb elements have common morphologic characteristics such as stout unit, broad cusp, and discrete denticles. M, Sa, Sb<sub>1</sub>, Sb<sub>2</sub>, Sc<sub>1</sub>, and Sc<sub>2</sub> elements possess long cusp, and thin process with long denticles. All elements possess distinct basal cavity.

Pa element: Paired segminate elements with arched and

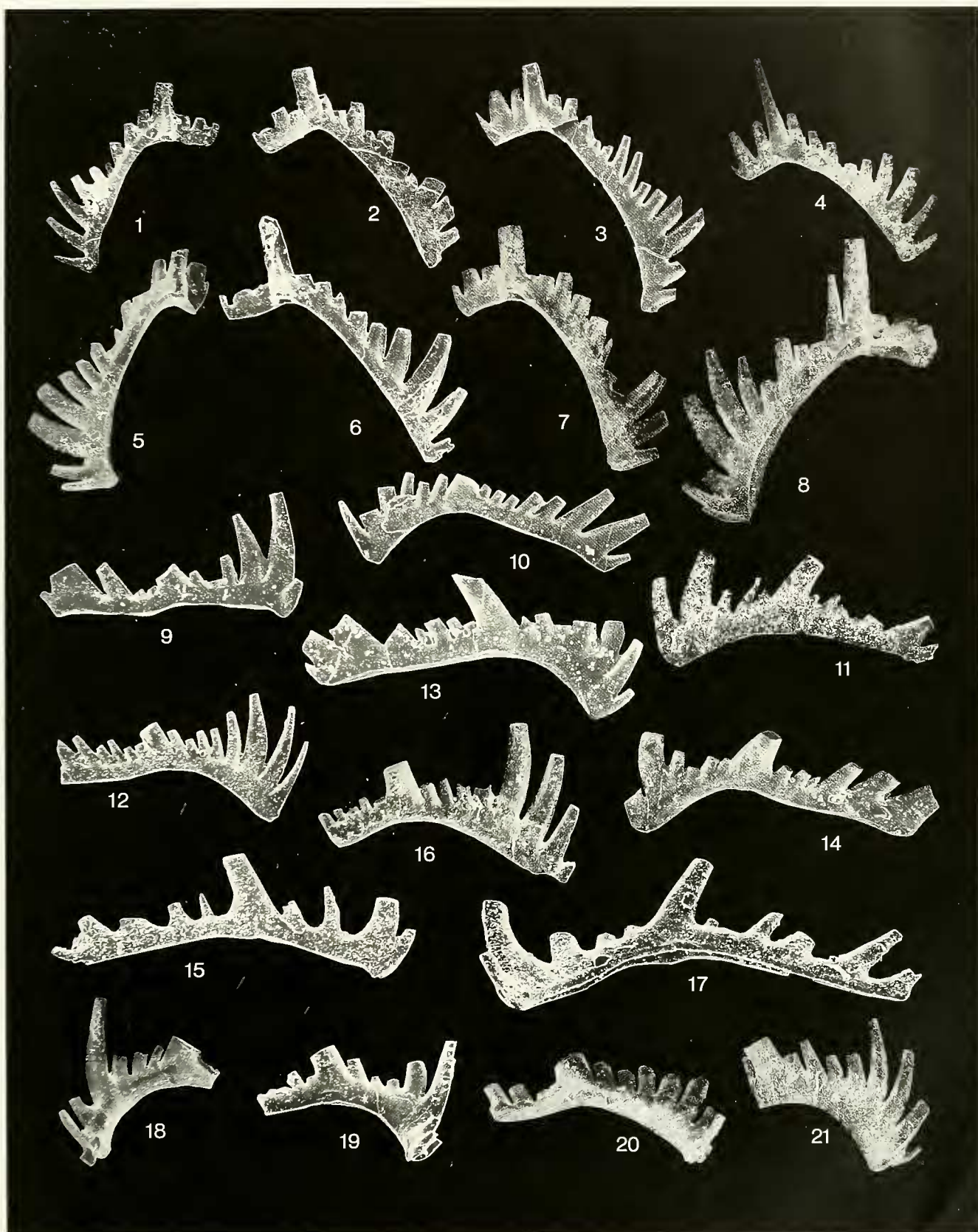
laterally curved process. Length of anterior process ranges from 250 to 720  $\mu\text{m}$ . Anterior process relatively low to high and carries 3 to 10 denticles. Denticles represent broad variation in denticulation and size: narrowly to broadly discrete and subequal to highly unequal in size. In the case of consisting of highly unequal denticles, they tend to become larger in central portion on anterior process in some specimens and become larger toward anterior in others. One or two denticles may be present behind cusp. Cusp shows a morphologic variation in relative size, shape, and degree of inclination: narrow to broad, short to long, and medium-angled to subparallel with anterior process. Basal cavity shallow, narrowly to widely expanded laterally. Basal cavity margin thin in immature form and tends to be thick in mature form. Basal groove narrow and extends from basal cavity to anterior end.

Pb element: paired angulate element with subequal anterior and posterior processes in length. Both processes meet at an angle of about 120 to 160 degrees in both upper and lateral views. Posterior process may be convex inward. Length of anterior and posterior processes ranges from 160 to 400  $\mu\text{m}$ , respectively. Denticles on anterior process 3 to 6 in number, short, discrete, and tend to increase in length and inclination posteriorly. Denticles on posterior process 3 to 6 in number, short, slender, discrete, and tend to increase in length and inclination posteriorly. Cusp large and stands commonly on anterior process and uncommonly on posterior process. Basal cavity a laterally compressed lenticular shape flaring outward in lower view. Basal groove extends anteriorly and posteriorly from basal cavity to beneath processes.

M element: Paired breviform digyrate elements with short and long lateral processes ranging from 60 to 140  $\mu\text{m}$  and from 530 to more than 670  $\mu\text{m}$  in length, respectively. Both processes meet at an angle of about 80 to 100 degrees in antero-posterior views. Short lateral process may be convex inward and carries 1 to 3 short denticles or none in some specimens. Long lateral process projects strongly downward and slightly convex outward. Denticles on long lateral process 8 to 10 in number, curve inward, and tend to increase in size and inclination downward. Cusp large and curves posteriorly. Basal cavity expanded posteriorly and slightly depressed on anterior side. Small lip of basal cavity present on posterior side and rounded keel extends from basal margin of lip to halfway up cusp. Narrow basal groove beneath both processes extends into basal cavity.

Sa element: Alate elements with two long lateral processes and long posterior process. Length of each lateral process ranges from 160 to 250  $\mu\text{m}$ . Length of posterior process unknown due to its incompleteness and more than 330  $\mu\text{m}$  in moderately large specimens. Lateral processes form an angle of 60 to 90 degrees with each other in anterior

→ **Figure 5.** Sb<sub>2</sub>, Sc<sub>1</sub> and Sc<sub>2</sub> elements of *Cratognathodus multihamatus* (Huckriede) from the Tahoe Formation. all  $\times 60$ . 1-8, Sb<sub>2</sub> elements, 1-2: YNUC15944-15945 from Lev. 1316. 3: YNUC15946 from Lev. 1321. 4: YNUC15947 from Lev. 1323. 5: YNUC15948 from Lev. 1321. 6: YNUC15949 from Lev. 1191. 7: YNUC15950 from Lev. 1321. 8: YNUC15951 from Lev. 1183. 9-17, Sc<sub>2</sub> elements, 9-15: YNUC15952-15958 from Lev. 1197. 16: YNUC15959 from Lev. 1193. 17: YNUC15960 from Lev. 1197. 18-21, Sc<sub>1</sub> elements, 18: YNUC15961 from Lev. 1127. 19: YNUC15962 from Lev. 1191. 20: YNUC15963 from Lev. 1322. 21: YNUC15964 from Lev. 1127.





view and 90 to 120 degrees with posterior process in lateral view. Denticles on each lateral process 3 to 5 in number, discrete, tend to be large in central portion. Inclination of denticles tends to increase toward cusp. Denticles on posterior process more than 11 in number, short, indiscrete and standing perpendicular. Cusp as long as largest denticle on lateral processes and slightly curves posteriorly. Basal cavity moderately expanded and narrow basal groove extends beneath lateral and posterior processes.

Sb<sub>1</sub> element: Paired breviform digyrate elements with subequal, long, slender lateral processes. Length of each lateral process ranges from 170 to 450  $\mu$ m. Both processes meet at an angle of about 90 to 120 degrees in upper view and are convex anteriorly. Denticles on each lateral process 7 to 10 in number, indiscrete, slightly inclined posteriorly, and tend to increase in length distally, the largest being the distalmost 2nd or 3rd. Cusp slender and as large as largest denticle on lateral processes. Basal cavity slitlike, narrow basal groove extends from basal cavity toward lateral processes.

Sb<sub>2</sub> element: Paired extensiform digyrate elements with short and long lateral processes. Length of short and long processes ranges from 130 to 200  $\mu$ m and from 460 to 640  $\mu$ m, respectively. Both processes meet at an angle of 100 to 130 degrees in antero-posterior views. Denticles on short lateral process 2 to 5 in number and tend to increase in length and inclination toward cusp. Denticles on long lateral process 10 to 13 in number, weakly curve posteriorly, and tend to increase in length distally, the largest being the distalmost 3rd or 4th. Inclination of denticles tends to increase toward cusp. Cusp slender, as large as large denticles on long lateral process, and slightly curves posteriorly. Basal cavity forms triangular shape in lower view. Small lip of basal cavity present on posterior side and narrow keel extends from basal margin of lip to approximately halfway up cusp. Narrow basal groove extends from basal cavity to beneath both lateral processes.

Sc<sub>1</sub> element: Paired bipennate elements with bifurcate long anterior process and long posterior processes. Length of anterior process ranges from 230 to 370  $\mu$ m. Length of posterior process cannot be measured because of its incompleteness. Anterior process bends at an angle of 30 to 80 degrees downward and 10 to 20 degrees inward. Denticles on anterior process 5 to 8 in number, tend to increase abruptly in size, being largest in anterior to middle portion, and then decreasing in size posteriorly. Bifurcation projects anterolaterally and forms an angle of about 160 degrees in both upper and lateral views and carries 1 to 3 small, discrete denticles. Posterior process may carry almost the same number of denticles as on anterior process. Cusp as long as longest denticle on anterior process. Basal cavity slitlike, narrow basal groove extends toward anterior and posterior processes.

Sc<sub>2</sub> element: Paired bipennate elements with long, slender anterior and posterior processes with long, discrete denticles. Length of anterior and posterior processes ranges from 300 to 470  $\mu$ m and 380 to 750  $\mu$ m, respectively. Anterior process bends at an angle of 30 to 80 degrees downward and 10 to 30 degrees inward. Denticles on

anterior process 5 to 9 in number and tend to be largest in anterior to middle portion and increase in inclination posteriorly. Denticles on posterior process 5 to 12 in number and tend to increase in size and inclination posteriorly. Basal cavity slitlike, very small lip of basal cavity turned upward on inner side. Narrow groove extends from basal cavity toward anterior and posterior processes.

*Remarks.*—The "ozarkodiniiform" element of *Celsigondolella watznaui watznaui* (Kozur) is somewhat similar to the Pa element of *Cr. multihamatus*. The former has, however, a conspicuously long cusp whose feature is out of the range of morphologic variation of the latter. The form species *Pollognathus sequence* (Kozur) and *P. germanicus* (Kozur) fairly resemble the Pa element of *Cr. multihamatus* but the former have a relatively long and slender cusp.

The holotype and other specimens of the form species *Ozarkodina saginata* illustrated by Huckriede (1958) are all incomplete and lack most of their posterior processes, which has caused some confusion in determination among angulate elements. The stout unit with relatively long discrete denticles of *O. saginata* shares characteristics with the Pb element of *Cr. multihamatus*. The holotype and another specimen of the form species *Cratognathodus posterognathus* (=the Pb element of *Cr. multihamatus*) shown by Mosher (1968) are of young forms of the form species *Or. saginata*.

One specimen figured as the form species *Lonchodina venusta* (=the M element of *Cr. multihamatus*) by Huckriede (1958) is incomplete and lacks the distal half of the longer lateral process but well represents such characteristic morphology as long denticles on the lateral process and broadly expanded basal cavity.

All specimens previously figured as the form species *Diplododela lautissima* and specimens determined by me as the Sa element of *Cr. multihamatus* lack most of their posterior processes. The Sa element can be distinguished, however, from the form species *D. magnidentata* (Tatge) by the anteriorly projecting lateral processes with long discrete denticles.

The specimens illustrated as the form species *Hindeodella stoppeli* by Bender (1967) are all incomplete but they appear to correspond to the Sb<sub>1</sub> element of *Cr. multihamatus* because of their "enantiognathiform" digyrate type with a broad angled junction of the lateral processes.

All specimens including the holotype of the form species *Lonchodina spengleri* (the Sb<sub>2</sub> element of *Cr. multihamatus*) are incomplete and lack most of the longer lateral process. The identification of this element is, however, not so difficult because of its extensiform digyrate type and the presence of a triangular basal cavity.

The holotype of the form species *Hindeodella petrae-viridis* (=the Sc<sub>1</sub> element of *Cr. multihamatus*) illustrated by Huckriede (1958) is of a part of the anterior process and lacks the bifurcation on the anterior processes. Therefore, some workers regarded this form species as bipennate type without the bifurcate anterior process or breviform digyrate types. The holotype possesses, however, a faint trace of the bifurcation on the basal part of the anteriormost denticle. Huckriede (1958) claimed that the form species *H. petrae-viridis* is characterized by the presence of the bifurcation on

the anterior process and four specimens figured by Huckriede (1958) carry distinct bifurcation. It is very difficult to distinguish  $Sc_2$  from  $Sc_1$  elements of *Cr. multihamatus* if the  $Sc_2$  elements are incomplete and lack the anterior portion of their anterior processes.

The form species *Prioniodella pectiniformis* erected by Huckriede (1958) is based on the specimens of a part of the posterior process with long discrete denticles. The features agree well with those of  $Sc_2$  elements of *Cr. multihamatus*.

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